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BIOLOGY OF THE PARTHENOGENETIC FUNGUS BEETLE *CIS FUSCIPES* MELLIÉ (COLEOPTERA: CIIDAE)

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Thelytoky, or female-producing parthenogenesis, has been reported for a large number of animal groups, and a considerable amount has been written on its occurrence in various groups of insects, such as the Psychidae, Aphididae, Tettigoniidae, Phasmidae, and Curculionidae (White, 1954; Suomalainen, 1962). Aside from the well known cases in *Ptinus clavipes* and several European weevils, there have been few references to thelytoky in the Coleoptera; yet this type of reproduction is probably fairly common throughout the order, judging from the number of groups in which unusual sex ratios have been noted. The step from the preliminary observation to experimental evidence is often a big one, however, because of the difficulties encountered in rearing many insects. While endeavoring to straighten out a taxonomic problem concerning some small fungus-feeding beetles in the family Ciidae, I discovered an apparent case of thelytoky in the species *Cis fuscipes* Mellié, and was able to confirm this by a series of rearing experiments discussed below. To my knowledge, this is the first record of its occurrence within the large superfamily Cucujoidea.

In connection with a study on the systematics and biology of western North American Ciidae, an attempt was made to distinguish between two apparent sibling species, *Cis fuscipes* Mellié and *Cis impressus* Casey. The two species are widespread in North America, have broadly overlapping distributions, and feed on the same species of fungi. The only characters given in the literature to separate the two are the form of the male pronotum and abdomen; in *C. impressus* the pronotum of the male is impressed anteriorly and the abdomen bears a setigerous pore on the first visible sternite, while both characters are apparently absent in the "male" of *C. fuscipes*. Females of the two species are apparently indistinguishable (Casey, 1898; Dury, 1917).

In an attempt to solve this problem, I examined about 1500 museum specimens from various parts of North America, collected large series of adults and larvae from both dimorphic and monomorphic populations in California, and dissected series from California and Minnesota, in order to examine genital characters. No characters could be found to separate females or larvae of the two species, nor could any external sexual characters be found in *C. fuscipes*. When dissections were made of relatively large samples, it was found that the monomorphic series consisted entirely of females. This led to the hypothesis that thelytoky was occurring in *C. fuscipes* and that the name *impressus* had been applied to male specimens of the same species. The following rearing experiments were then conducted.

REARING EXPERIMENTS

Larvae of *Cis fuscipes* and fresh pieces of *Polyporus versicolor* were collected in Marin Co. and Alameda Co., California. Each larva was isolated in a petri dish with a piece of fungus, and water was added from time to time. Each resulting female was kept in isolation and observed periodically for the presence of eggs and larvae. Several rearings were attempted, but only one will be discussed here. One larva was isolated on December 9, 1962, and by January 26, 1963, it had pupated and eclosed, producing an adult female. By February 7, eggs had been laid and early instar larvae were seen boring in the fungus. By April 1, 15 females were seen in the medium; 7 of these were preserved, while the other 8 were isolated in separate dishes. Eggs were seen in most of these dishes by May 4, and on May 31, all the adult females were removed and preserved, leaving only the F_2 larvae in the dishes. By July 19, adult F_2 females were present in all 8 dishes. Five of the clones were preserved, and the numbers of individuals contained in each were as follows: 51, 50, 43, 42, and 47. The remaining clones produced an F_3 generation by October 24, and one of these was retained to produce F_4's by the end of the year.

Because of intermittent field work, the exact generation time could not be recorded, but the F_1 generation was produced in about 60 days, which appears to be a reasonable figure when compared with observations made on several other ciid species.

Two attempts were made to cross females from these parthenogenetic clones with males collected in the same area; all of these were unsuccessful in that only female progeny resulted. Mating probably did not take place, but many more trials will be necessary before one can conclude that parthenogenetically-produced females will not cross with males from bisexual populations.

It is obvious that some form of thelytoky is occurring in this species, but the actual cytological mechanisms involved have not been studied. Chromosome counts made by Mr. Norihiro Ueshima showed that the diploid number is 14 both in the male and in the parthenogenetic female. Thus polyploidy does not occur in the California populations examined.

GEOGRAPHICAL AND ECOLOGICAL RANGE

Cis fuscipes is the most widespread and common species of Ciidae in North America, ranging from northern British Columbia to southern California on the Pacific Coast, east across southern Canada to Nova Scotia, and south throughout the eastern and midwestern United States (east of the 100th meridian) to Brownsville, Texas, and Dunedin, Florida (Fig. 1). It is apparently absent from the more arid parts of the continent, such as the Great Plains, the Great Basin, and the southwestern deserts. A single record from Provo, Utah, indicates its possible occurrence in the poorly collected Rocky Mountain region. Specimens have also been seen from Mexico (no specific locality), Cuba, Hawaii, and from the island of Madeira in the eastern Atlantic. These isolated records will be discussed below.

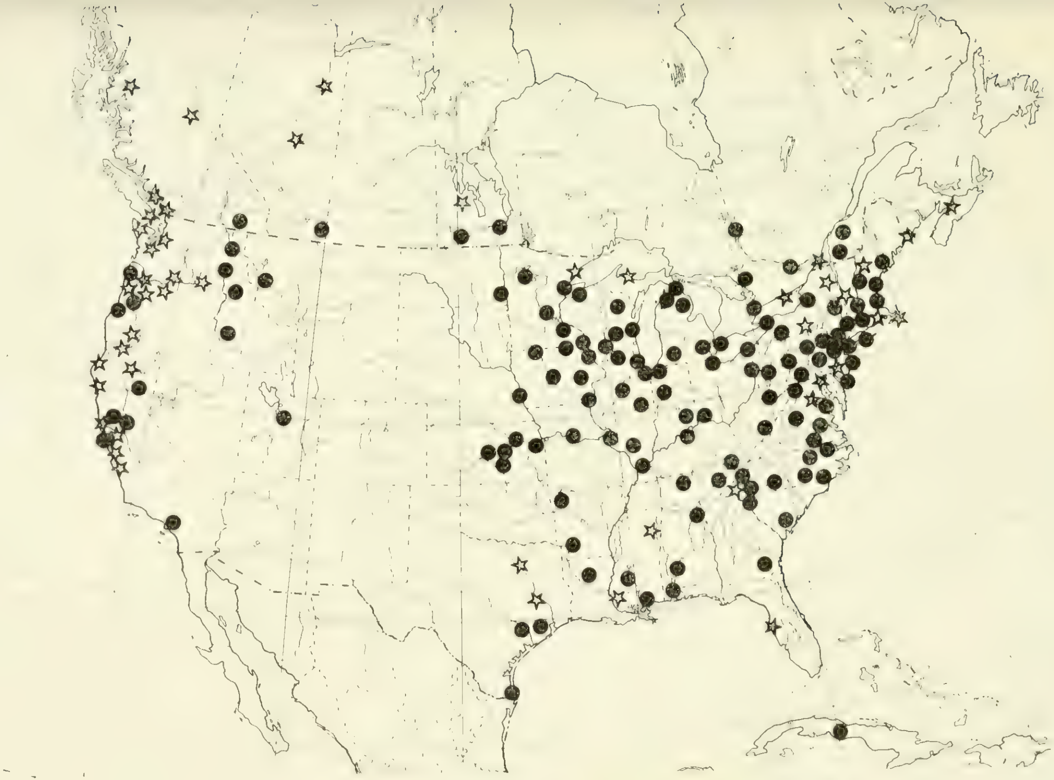
Throughout its range, the species occurs in association with several species of bracket fungi (Basidiomycetes: Polyporaceae), where both adults and larvae feed within the fruiting bodies. It appears to be restricted to members of the *Polyporus versicolor* group (Paviour-Smith, 1960), which have small, relatively thin sporophores with whitish, punky context and a trimitic hyphal system and which usually cause white rot in dead or dying angiosperms. It is especially common in *Polyporus versicolor,* which may be considered its "headquarters" (Elton, 1949; Paviour-Smith, 1960), but also feeds on related fungi. Out of the 92 host records which I have accumulated for this species, 72 are from *P. versicolor,* 7 from *P. hirsutus,* 6 from *Lenzites betulina,* 2 from *P. conchifer,* and a single record each from *P. squamosus, Trametes suaveolens, Fomes fraxineus, Ganoderma brownii,* and *P. gilvus.*

In the western part of its range, *Cis fuscipes* is usually found associated with *Cis versicolor* Casey, *Cis vitulus* Mannerheim, *Sulcacis curtulus* (Casey), *Ennearthron californicum* Casey, and *Octotemnus laevis* Casey. In California, extensive collecting has revealed that *C. fuscipes* (as well as *C. vitulus* and *O. laevis*) requires a somewhat more humid environment than *C. versicolor, S. curtulus,* or *E. californicum,* and it may be replaced by these species in drier environments. In the eastern part of its range, the species occurs with a number of other ciids, including *Cis pistoria* Casey, *Cis falli* Blatchley, *Sulcacis lengi* Dury, *Strigocis opacicollis* Dury, and *Octotemnus laevis* Casey, and other fungivorous beetles, such as *Neomida bicornis* (Fabricius) and *Euparius marmoreus* (Oliviér). It is relatively common in most areas and appears to be successfully competing with other species inhabiting the same fungi.

Like many species of polypores, *P. versicolor* and its relatives are widely distributed and are found on many different tree species, although they are normally restricted to angiosperms. One might expect a fairly continuous distribution of these fungus species within any deciduous forest, but the actual occurrence of fruiting bodies will depend upon the forest composition, number of dead trees, and physical factors affecting the establishment of the fungus and the production of sporophores. Even in a continuous forest, one may find *P. versicolor* replaced in certain areas by *P. gilvus* or *P. pargamenus,* each of which support different ciid species. This breaking up of the habitat will be more evident, of course, where the hardwoods themselves are scattered or rare. The absence of *Cis fuscipes* from the more arid part of western North America may be due to the inability of the species to tolerate drier environments, as was suggested by observations on California populations, rather than to the lack of hardwood forests, or to physical factors affecting the host fungi. The relative rarity of the beetle in the more humid parts of the Sierran and Cordilleran ranges, however, may be related to the scattering of the habitat, since large stands of conifers separate riparion situations in which alders and other angiosperms provide a suitable medium for the host fungi.

DISTRIBUTION OF BISEXUAL POPULATIONS

The abundance of male specimens varies considerably throughout the range of this species. Since intensive population sampling was not attempted, it is not possible to present a detailed analysis of the sex ratios, but a general idea of the distribution of bisexual populations may be derived from the data recorded for over 2500 specimens (from 405 localities) collected by myself or borrowed from various museums. For the entire range, 12 per cent of the specimens examined were males, and these represented 21.7 per cent of the localities. In Figure 1, the localities from which



FIGURE

Map of the New World distribution of *Cis fuscipes* Mellié. Black circles represent localities from which only females have been recorded; stars indicate the presence of at least one male in the series.

males were taken are represented by stars, while those from which only females were recorded are represented by black dots. Two things that are immediately apparent are: 1) the preponderance of male records in the northwestern part of the continent, as compared to their rarity on the east coast and complete absence in the Midwest, and 2) the scattered occurrence of males throughout the range as far south as Florida and Texas. From California, Oregon, Washington, British Columbia, and Alberta, 918 specimens (36.2%) from 77 localities (19.0%) were examined, and of these 221 specimens (24.1%) from 51 localities (66.2%) were males. From the remainder of Canada and the United States, 1618 specimens (63.8%) from 328 localities (81.0%) were examined, and of these 84 specimens (5.2%) from 37 localities (12.7%) were males. Of the total male specimens examined, 72.4 per cent were collected in the Pacific states and western provinces.

Although the sample sizes vary greatly and were often small, (decreasing the reliability of negative evidence), I think there is little doubt that bisexual populations are more abundant in the Northwest and become increasingly rare to the east and south. Parthenogenetic populations occur throughout the range, and in northern coastal California both types appear to be common in any one area. Males have been taken at several localities along the east coast and in the Gulf Coast states, but I have seen no records of their occurrence in the Midwest.

SYSTEMATIC RELATIONSHIPS AND PROBABLE ORIGIN

Cis fuscipes is closely related to a group of Old World species which were placed in the subgenus *Hadraule* Thomson by Reitter (1902), Chujo (1939), Miyatake (1954), and others. The name *Hadraule,* however, does not apply to the group, since its type species, *Cis elongatulus* Gyllenhal, has been excluded (Lohse, 1964; Lawrence, 1965). The species seem to form a natural unit and are characterized as follows: stout, oblong to subparallel body form; pronotum with fairly broad lateral margins and produced and rounded apical angles, which are preceded by a lateral inflexion of the disc; dual and subseriate elytral punctation; vestiture of stout, erect bristles; prosternum slightly tumid but not carinate; apex of the protibia strongly dentate; and the male with two weakly developed clypeal plates, anteriorly impressed pronotum, setigerous pore on the third abdominal sternite, and relatively simple aedeagus. The species group extends from eastern

Siberia through southeastern Asia and India to Africa and Madagascar, being absent in northern Africa and Europe, but the species which most closely resemble *C. fuscipes* occur mainly in Siberia and Japan. These include *Cis seriatopilosus* Motschulsky (Siberia: Amur, Sakhalin; Japan); *Cis seriatulus* Kiesenwetter (Japan); *Cis heiroglyphicus* Reitter (Siberia: Khabarovsk; Japan); *Cis taiwanus* Chujo (Taiwan, Loo Choo Islands, Japan?); *Cis subrobustus* Miyatake (Japan); and *Cis japonicus* Nobuchi (Japan).

Those species which have been studied biologically occur on the same fungi as *C. fuscipes. Cis seriatopilosus* and *C. taiwanus* have both been recorded from *Polyporus versicolor,* while *C. subrobustus* has been collected on *P. hirsutus* (Chujo, 1939; Fukuda, 1940; Miyatake, 1954). Although most of these beetles appear to be specifically distinct from the North American species, a single Siberian specimen identified by Reitter as *C. seriatopilosus* is very similar to individuals of *C. fuscipes.* Perhaps further collecting in eastern Siberia will reveal the presence of *fuscipes* there.

The presence of several close relatives in Asia and the abundance of males in the northwestern part of the range suggest that *Cis fuscipes* or its ancestor dispersed into North America across the Bering Strait from a point of origin in the eastern Palaearctic. Since there is no evidence of unusual sex ratios among the Japanese and Siberian species, it is probable that the parthenogenetic mode of reproduction originated in northwestern North America and the species subsequently spread east and south across most of the continent.

In the absence of a fossil record, there is no direct evidence relating to the time of dispersal of *C. fuscipes* into North America. Some indirect support may be derived from Linsley's analysis of the cerambycid beetle fauna (1958), in which he considers all of the northern or Holarctic elements of the fauna to be post-Pleistocene in origin. Several of the examples of thelytoky in animals have been demonstrated to be glacial phenomena; this is discussed by Suomalainen (1962) for insects, and by Darewski and Kulikova (1961) for lacertid lizards. The recent origin of parthenogenesis has been argued by some authors on theoretical grounds, because of the inherent long-term disadvantages of this type of genetic system.

SPREAD AND OVERSEAS DISPERSAL

The ability of a parthenogenetic species to colonize and spread rapidly throughout a new area is well known and has been discussed in various texts, such as White (1954), and Mayr (1963).

A system which suspends sexual reproduction not only makes possible the perpetuation of a successful genotype as soon as it is formed, but doubles the fecundity by eliminating the "reproductive wastage" characteristic of a population in which roughly half of the individuals are males. Where the suitable habitat for a species is broken up, a parthenogenetic form will be able to spread more rapidly, since only a single female need reach a favorable microenvironment. In an area which is initially unsuitable for a bisexual species, the development of a parthenogenetic system may speed up the process of adaptation to the new environment by immediately fixing and reproducing a favorable genotype. Stebbins (1950) and others have stressed the importance of apomixis in the rapid colonization of new habitats by plant species.

A comparison of the ranges of North American Ciidae shows that only *Cis fuscipes* occurs throughout the northern part of the continent and yet is also an important element in the fauna of the southeastern and midwestern United States. Several other species have northern distributions and similar affinities to Palaearctic species. Some of these, such as *Cis horridulus* Casey and *Dolichocis indistinctus* Hatch extend southward only in montane regions and may occur in the southern Appalachians or in the mountains of Arizona. *Sulcacis curtulus* (Casey) extends into southern California but is rare in the northeastern and northern midwestern states. *Eridaulus levettei* (Casey) is fairly widespread in the eastern part of the continent, but does not occur in the West, while *Octotemnus laevis* Casey is common along both coasts and in parts of the Midwest. Neither of these species is as common or widespread as *C. fuscipes,* and both are absent from the Southern Coastal Plain and Gulf Coast. Two other wide-ranging species, *Ennearthron californicum* Casey and *Ennearthron thoracicorne* (Ziegler), occur in the western and eastern states respectively. Both of these, however, are of southern origin, having their closest relatives in the Neotropical Region, and neither extends far into Canada. The comparison of *C. fuscipes* with other northern or Holarctic members of the North American fauna may seem to imply that all of these have similar relationships to Palaearctic species and thus represent Old World invasions of roughly the same age. This does not appear to be the case. All of the other northern species have Old World counterparts which extend throughout the Palaearctic from Europe to Siberia and Japan, whereas only *C. fuscipes* belongs to a group restricted to the eastern Palaearctic and Oriental regions and having some relationships with palaeotropical forms. It may be that *C. fuscipes* represents the most recent element in our fauna, but there is no direct evidence for this.

I think there is little doubt that the evolution of thelytoky in *C. fuscipes* is responsible for the apparently rapid spread of the species and for its present wide distribution in North America. In addition to the obvious advantages of the parthenogenetic system to dispersal and colonization, the increased fecundity has probably contributed to its success in competing with the large and diverse fauna of southern origin occupying the southern periphery of the range. The only large area in North America which is suitable for *C. fuscipes,* but in which the forest cover is considerably broken up, due partly to agriculture, is the Midwest. It is interesting that this is the only region in which males are totally absent.

The presence of males in scattered localities along the east coast and at the southern extremities of the range raises several questions which can be answered only by more detailed population studies. Is the parthenogenetic form the result of a single evolutionary event, an obligate thelytokous form being completely independent of the bisexual form? Is a residual bisexual population continually giving rise to parthenogenetic clones? Is parthenogenesis facultative in this species, so that occasional females can give rise to normal males? It is hoped that future studies will provide the answers.

Mellié's original series of *Cis fuscipes* included several specimens from the island of Madeira. It would seem improbable that the Madeiran series represents the same species, but an examination of Mellié's and Wollaston's specimens revealed that they are conspecific with the North American *fuscipes,* and that they are all females. According to Wollaston (1854, 1865), the species has become well established in cultivated areas at low elevations around Funchal and is likely to be an accidental introduction. Although it is possible that a specimen of *fuscipes* could have rafted from the Caribbean to Madeira, it is more reasonable to assume that the species was introduced by man.

Recently, a series of female specimens of *fuscipes* were collected at Olinda on the island of Maui, Hawaii, and presented to the Commonwealth Institute of Entomology. Although Perkins, Swezey, and others have collected extensively in Hawaii, this is the first record of this species there, and probably represents a recent human introduction. In addition to this, two female specimens in the Reitter collection were apparently collected in Cuba. Whether by natural means or by human transport, *Cis fuscipes* has dispersed from North America to these various islands, and has become established on at least one of them. The advantages of parthenogenesis in the establishment of a species having been introduced into a new area by long-distance dispersal have been discussed by several authors, including Longhurst (1955) for Crustacea, and Baker (1955) for plants.

TAXONOMIC STATUS

Because of its variability and wide distribution, *Cis fuscipes* has been given a number of names by different authors. Mellié (1848) described the species from a series of 5 specimens from Boston in the Chevrolat collection and 4 more collected by Wollaston on Madeira. In the same paper, three other names were applied to the species: *Cis atripennis,* also from Boston, *Cis chevrolatii* from "Nouvelle-Orleans," and *Cis dubius* from the latter locality. Leconte, Horn, and others applied the name *fuscipes* to the common North American species, and it has been used consistently by later authors. Casey (1898) described two more species, *Cis carolinae* (North Carolina) and *Cis pallens* (Montana), which were distinguished from *fuscipes* on the basis of color and relative lengths of antennal segments. He also described a third species, *Cis impressus* (Pacific Coast), differing from *fuscipes* only in the form of the male pronotum, which was said to be "broadly impressed at apex." Dury (1917) noted that *Cis fuscipes* occurred throughout North America, that *C. impressus* occurred on both coasts, and that the females of the two species could not be distinguished from one another. He also considered *chevrolatii* and *carolinae* to be synonyms of *fuscipes.*

During the summer of 1963, I examined the Casey types at the United States National Museum, Washington, D. C., and in the spring of 1966 I had the opportunity to study the types of Mellié in the Sallé and Pic collections at the Muséum National d'Histoire Naturelle, Paris, and in the Wollaston collection at the British Museum (Natural History), London. All of the above names, with the exception of *Cis impressus* Casey, are based on female specimens of the variable *Cis fuscipes.* The name *fuscipes* is here selected as the senior synonym because of its continual usage in the North American literature. Being based on a bisexual population, Casey's name *impressus* presents certain difficulties. Since it has not yet been established whether this species is facultatively parthenogenetic or rather composed of a bisexual species and one or several obligate parthenogenetic clones, it could be argued that the name *impressus* should be applied to populations in which males occur. The true nature of the biological situation will be made clear only after intensive population analyses, rearing experiments, and cytological studies. In any case, I prefer to consider *impressus* a synonym of *fuscipes* on purely practical grounds, since no characters have been found to distinguish the larvae or females of the two forms. I therefore propose the following synonymy:

CIS FUSCIPES Mellié

Cis fuscipes Mellié, 1848: 271, pl. 2, fig. 23; Wollaston, 1854: 281; Wollaston, 1865: 234; Casey, 1898: 78; Blatchley, 1910: 898; Dalla Torre, 1911: 11; Dury, 1917: 11; Leng, 1920: 246; Weiss, 1920: 138 (host); Weiss and West, 1920: 8 (host); Weiss and West, 1921b: 169 (host); Böving and Craighead, 1931: 270-71, pl. 92, figs. K-R (larva); Arnett, 1962: 827, fig. 1.98; Hatch, 1962: 231; Lawrence, 1965: 279. Type locality: "Boston." Lectotype, female, Pic collection, Mus. Natl. Hist. Nat., Paris.

Cis atripennis Mellié, 1848: 258, pl. 2, fig. 15; Casey, 1898: 77; Dalla Torre, 1911: 6; Leng, 1920: 246. Type locality: "Boston." Holotype, female, Pic collection, Mus. Natl. Hist. Nat., Paris. NEW SYNONYMY.

Cis chevrolatii Mellié, 1848: 249; Blatchley, 1910: 898; Dalla Torre, 1911: 8; Dury, 1917: 11; Leng, 1920: 246. Type locality: "Nouvelle-Orleans." Lectotype, female, Pic collection, Mus. Natl. Hist. Nat., Paris.

Cis dubius Mellié, 1848: 273; Dalla Torre, 1911: 10; Leng, 1920: 247. Type locality: "Nouvelle-Orleans." Lectotype, female, Salle collection, Mus. Natl. Hist. Nat., Paris. NEW SYNONYMY.

Cis carolinae Casey, 1898: 78; Dalla Torre, 1911: 8; Dury, 1917: 11; Leng, 1920: 246. Type locality: "North Carolina (Asheville)." Holotype, female, Casey collection, U.S. Nat. Mus., Washington, D.C.

Cis impressa Casey, 1898: 79; Dalla Torre, 1911: 12; Dury, 1917: 11; Blatchley, 1918: 54; Leng, 1920: 246; Weiss and West, 1921a: 61 (host); Blatchley, 1923: 19; Hatch, 1962: 231. Type locality: "Vancouver Island." Holotype, male, Casey collection, U. S. Nat. Mus., Washington, D. C. NEW SYNONYMY.

Cis pallens Casey, 1898: 78; Dalla Torre, 1911: 15; Leng, 1920: 246. Type locality: "Montana (Missoula)." Holotype, female, Casey collection, U. S. Nat. Mus., Washington, D. C. NEW SYNONYMY.

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